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Response to Selection for Grain Filling Capacity in Wheat (*Triticum aestivum* L.) under Heat Stress

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ABSTRACT

Improving tolerance to heat stress of bread wheat has been achieved through enhancing grain filling capacity by two cycles of selection imposed on five F_2 populations derived from crosses among long spike–equally tall inbred lines quite variable in 1000 kernel weight (1000 KW). The first cycle was a divergent selection for 1000 KW conducted under the high temperature of a late rowing date at an intensity of 5% and the responses were measured in favorable and heat stress environments. Significant positive responses were obtained in the five populations in the two contrasting environments. Selection for higher 1000 KW resulted in greater response under heat stress (averaged 6.9% of population mean) than under favorable conditions (averaged 4.92%). The F_3 families selected for higher 1000 KW were less sensitive to high temperature as they displayed less reductions due to heat stress (averaged 5.55%) than the unselected bulks (7.14% average reduction) relative to the performance under favorable conditions. The responses to selection for lower 1000 KW were greater under the favorable conditions (averaged 5.6%) than under heat stress (averaged 4.12%). Significant concurrent positive responses were obtained in stem diameter with selection for higher 1000 KW which was greater under heat stress (averaged 8.82%) than under favorable conditions (averaged 4.51%). Directional selection for stem diameter imposed on the plants of the F_3 families in the second cycle resulted in significant positive responses in the five populations which averaged 16.24% of population mean as well as concurrent responses in 1000 KW (averaged 16.01%) and in grain yield /spike (averaged 19.5%). Selection for 1000 KW under heat stress produced concurrent response in stem diameter and vice versa which implies that the two characters are closely related. Increasing stem diameter by selection was more efficient than selection for 1000 KW in enhancing grain filling capacity through providing greater storage of stem reserves of water soluble carbohydrates to be remobilized into the developing grains under high temperature.

INTRODUCTION

The global increase in temperature occurring since the beginning of this century which is predicted to continue in the future (Hansen *et al*., 2012) forms a serious constraint to wheat productivity. The adverse effects of high temperature are more detrimental when it coincides with grain filling stage (Blum *et al.*,1994). Wheat in Egypt is planted in late autumn and reaches grain filling in spring when temperature starts to rise with ensuing heat waves lasting for several days. Short heat waves (>30C°) during grain filling reduce grain size, consequently yield by depressing photosynthesis (Al-Khatib and Paulsen,1999) and suppressing sugar supply to the developing grain in addition to inducing premature senescence of the grain (Shirdel Moghanloo *et al*., 2016) Every day above 30C° at or around flowering caused 15% loss in yield (Telfer *et al*.,2013). The impact of heat stress on grain size was found to be mainly due to significant narrowing of the grains while their length remained unchanged (zhang *et al*., 2017). Evidently, with starch makes up to 70% of grain mass (Jenner, 1994) reduced sugar supply to the developing grain and impaired conversion of sugar into starch due to heat stress account for such reductions in grain size. The ability of the plant to maintain grain number and grain size under heat stress were found to be the most significant traits in plant response to high temperature (Kuchel *et al*., 2007). With the accelerated senescence of leaves and suppressed photosynthesis under heat stress, the wheat plant relies for grain filling on stem reserves of water soluble carbohydrates (WSC) stored before anthesis (Blum,1998) which constitutes up to 60% of grain dry matter under high temperature (Bidinger *et al*.,1977). The potential for storage WSC is determined by stem volume which comprises both stem length and diameter (Blum, 1998). Apparently short stem limits the capacity of the plant to store WSC (Borrel *et al*., 1993 and Ehdaie *et al*., 2006). Evidently; with most of the modern cultivars of wheat have short stems the only avenue open to increasing the stem volume is through selecting for larger stem diameter which is a highly heritable trait (Yao *et al* 2012, and Omara *et al*., 2009) and closely related to grain weight and yield under heat stress (Farrage *et al*., 2015) since it is closely correlated with number of vascular bundles in the stem which constitutes the storing sites for WSC. In the present study enhancing grain filling capacity has been approached through applying two successive cycles of phenotypic selection to five F_2 populations of wheat. The first cycle was directed to selecting for single grain mass as monitored by 1000 KW and measuring the concurrent responses in stem diameter. The second cycle was applied to the F_3 plants resulting from the first cycle to select for stem diameter and for measuring the correlated responses in 1000 KW and grain yield/spike.

MATERIALS AND METHODS

From an array of 100 recombinant inbred lines (F_{14}) derived by single seed descent from a cross between the long spike L 15 x land race WK-4, Seven lines parental equally tall (>120 cm) long spike lines (>18 cm) were chosen which were quite variable in 1000 KW.

Five crosses were established among the seven parental long spike lines which were as follows:

Cross No.	Parents	1000 KW of parents
Cross 1	Line 14 x Line 4	High x Medium
Cross 2	Line 4 x Line 8	Medium x Medium
Cross 3	Line 8 x Line 3	Medium x Medium
Cross 4	Line 58 x Line 11	Medium x Medium
Cross 5	Line 7 x Line 8	High x Medium

In 2014-2015 wheat growing season, a total of 100 F_2 plants of each cross were planted in the field of the Experimental Farm of Assiut University at a late sowing date (30^{th} of December) as spaced plants (30 cm between plants in rows set 30 cm apart). The following characters were scored for each individual plant:

1- Stem diameter (mm) of the second basal internode of the main culm.
2- 1000 Kernel weight (g)

Selection procedure:

Two successive cycles of phenotypic selection were carried out.

The first cycle was a divergent selection for 1000 KW among the F_2 segregates of the five populations in which the highest five plants and the lowest five in 1000 KW were selected (5% intensity). Equal numbers of seeds from the 100 F_2 plants were pooled for each population in order to form the F_3 bulk (non-selected). In the next season (2015-2016) wheat growing season, the F_3 selected families along with their relevant bulk were sown into the field of the Experimental Farm of Assiut University in two environments, namely a favorable environment of a normal sowing date (28th of November 2015) and a heat stress environment of late sowing date (30th of December 2015). A randomized complete block design (RCBD) was used and each selected family as well as five bulk families was represented in each of three replicates by a row of ten plants spaced 30 cm apart in rows set 30 cm from each other. Stem diameter (mm) grain yield per spike (g) and 1000 KW (g) were scored for each individual plant.

The second cycle of selection was a directional selection for large stem diameter from within F_3 families selected for 1000 KW. The top three plants in stem diameter among the 30 F_3 plants of each family (plants pooled over blocks) were selected (an intensity of 10%). The F_4 selections along with their relevant un-selected bulks were sown into the field in a late sowing date (30th December) of 2016-2017 wheat growing season in a RCBD with three replicates. Each of the three selected F_4 families along with the relevant three bulk families of each population was represented in each block by a ten –plant row with plants spaced 30 cm abort in rows set 30 cm from each other. The three main characters, namely stem diameter, grain yield per plant and 1000 KW were recorded for each individual plant.

Temperature at experimental site:

The maximum daily air temperatures at the experimental site (Fig.1) fluctuated between 21 to 42C° in March and between 20 to 42C° in April in the three successive years of 2015 through 2017 (weather reports in Assiut, whttps//: W under ground.com). Several heat waves (>35C°) occurred during the post anthesis –grain filling stage of plant development in March and April for each year.

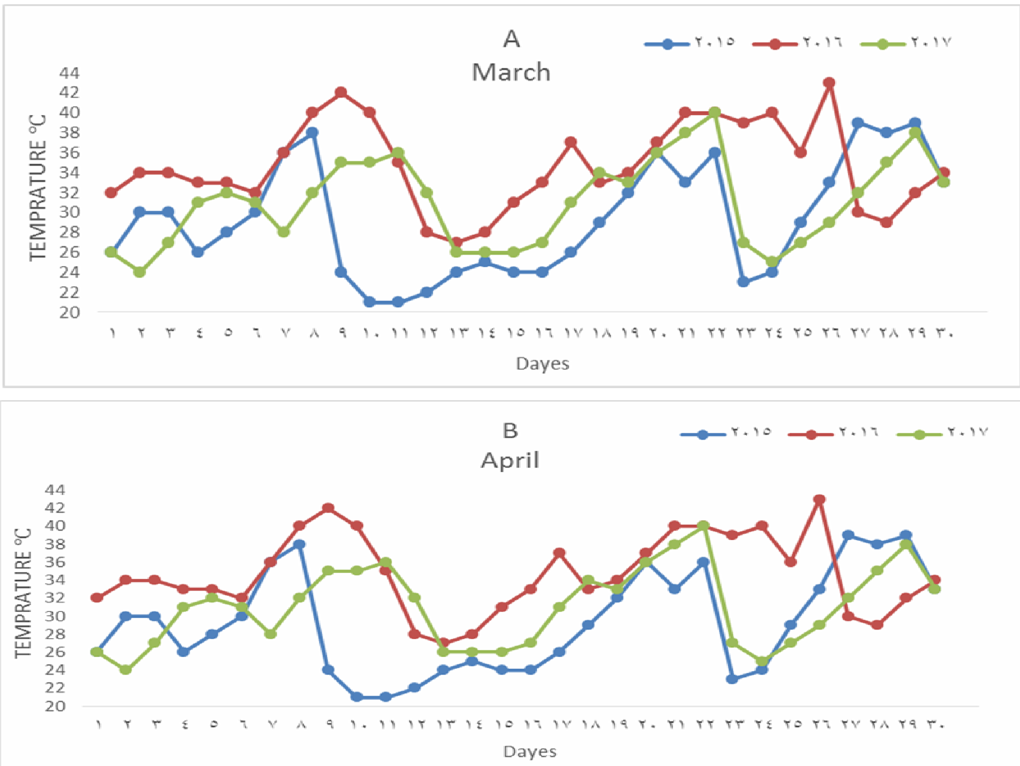


Figure 1. Maximum daily air temperature (C°) recorded at the experimental site during March (A) and April (B) of 2015, 2016 and 2017.

RESULTS AND DISCUSSION

Results: -

The F_2 segregates of the five populations displayed continuous and almost normal distributions for 1000 KW under heat stress (Figs. 2-6) indicating the quantitative nature of the trait and the polygenic control over it. The selection differentials (Table 1) were of comparable values in the five populations in the high direction ranged from 9.22 to 15.00 g but of wider range in the low direction ranged from 4.03 to 17.90 g. However, the averages of selection differentials over populations were almost comparable in the two directions (12.26 vs.9.54 g). The impact of heat stress on 1000 KW was quite remarkable with the unselected bulks being the most affected (an average reduction of 7.14%) followed by the low selection (5.71%) while, the high selections were the least affected (5.55%)

Response to divergent selection for 1000 KW.

The five populations responded positively and significantly to the selection pressure applied under heat stress in the two test environments (Table 2). Under the heat stress environment, the response in the higher 1000

KW direction ranged from 5.52 to 8.45% of population mean with an average of 6.90% which were greater than those obtained in the favorable environment ranged from 2.2 to 9.06% with an average of 4.92%. In contrast, the response in the lower 1000 KW direction was less under heat stress and ranged from 2.48 to5.74% with an average of 4.12% than those obtained under favorable conditions ranged from 3.22 to 9.03% with an average of 5.63%. The % response in each of the two environments was almost symmetrical for high and low directions with only one exception (pop.4), low to moderate realized heritability estimates were obtained under heat stress ranged from 0.19 to 0.45 as well as under favorable conditions ranged from 0.11 to 0.45. Meanwhile, the parent – offspring regression values measuring narrow-sense heritability were greater being 0.34 to 0.62 under heat stress and 0.33 to 0.55 in the favorable environment.

Table 1. Means of 1000 KW (g) of the five F_2 populations under heat stress conditions with the means of the F_2 plants selected for higher and lower 1000 KW and the selection differential.

Pop. No.	F_2 populations	Means of selected F_2 plants		Selection differential	
		High	Low	High	Low
1	60.30	70.50	42.40	10.20	17.90
2	57.25	71.35	50.00	14.10	7.25
3	56.70	69.40	51.10	12.70	5.60
4	58.40	67.62	45.75	9.22	12.65
5	54.10	69.20	49.80	15.10	4.30
Average	57.35	69.61	47.81	12.26	9.54

1st cycle of selection

Table 2. Response to selection % for 1000 KW in the high and low directions together with the realized heritability (h²) and parent-offspring regressions (bpo) in favorable and heat stress environments.

Pop. NO.		Favorable envir. Mean	Favorable envir. Response %	Heat stress Mean	Heat stress Response %
1	Bulk	58.79		54.09	
	High	62.45	6.22**	58.66	8.45**
	Low	55.83	5.02**	50.98	5.74**
	h²	0.36		0.45	
	bpo	0.45*±0.062		0.62**±0.03	
2	Bulk	53.70		51.50	
	High	55.81	3.92**	54.78	6.35**
	Low	51.97	3.22**	50.22	2.48*
	h²	0.15		0.23	
	bpo	0.33*±0.120		0.34*±0.15	
3	Bulk	59.47		50.81	
	High	65.21	9.06**	54.29	6.85**
	Low	55.83	6.61*	49.19	3.18**
	h²	0.45		0.27	
	bpo	0.55**±0.133		0.55**±0.13	
4	Bulk	57.16		51.38	
	High	58.37	2.20*	55.16	7.35**
	Low	51.95	9.03**	49.00	4.62*
	h²	0.13		0.41	
	bpo	0.35*±0.145		0.56*±0.16	
5	Bulk	49.98		51.38	
	High	51.58	3.21**	54.22	5.52**
	Low	47.83	4.29**	49.00	4.61**
	h²	0.11		0.19	
	bpo	0.40*±160		0.38*±0.18	

* P < 0.05 ** P < 0.01

Correlated response in stem diameter.

The divergent phenotypic selection for 1000 KW produced concurrent positive responses in stem diameter (Table 3). Under favorable conditions, the correlated responses in the high direction ranged from 6.17 to 9.15% with an average of 7.06 % of population mean, whereas under heat stress the correlated responses ranged from 7.55 to 10.93 % with an average of 9.20% of population mean. Meanwhile, the correlated responses (CR) in the low 1000 KW direction ranged from 4.40 to 5.31% with an average of 4.72% in the favorable environment and from 3.59 to 7.49% with an average of 5.69% under heat stress. The differences between the plants with large stem diameter and those with small stem diameter were quite visible in the field (Figure 6).

Table 3. Correlated response to selection for 1000 KW in the high and low directions in stem diameter under favorable and heat stress.

Pop. No.	Population type	Favorable environment mean	Favorable environment Correlated response (%)	Heat stress. mean	Heat stress. Correlated response (%)
1	F_3 bulk	5.60		4.94	
	High	5.95	6.35**	5.48	10.93**
	Low	5.35	4.45	4.61	6.68**
2	F_3 bulk	5.00		5.00	
	High	5.31	6.20**	5.43	8.60**
	Low	4.78	4.40**	4.82	3.59**
3	F_3 bulk	5.35		4.96	
	High	5.75	7.47**	5.41	9.07**
	Low	5.08	5.04**	4.59	7.45**
4	F_3 bulk	4.70		4.75	
	High	5.13	9.15**	5.22	9.89**
	Low	4.45	5.31**	4.52	4.84**
5	F_3 bulk	5.18		4.90	
	High	5.50	6.17**	5.27	7.55**
	Low	4.95	4.44**	4.61	5.90**

* P < 0.05 and ** P < 0.01

2nd Cycle of selection

The selection differentials of the five F_4 populations were ranging from 0.68 to 1.57 mm with an average of 1.03 mm (Table 4). The directional selection for greeter stem diameter which was imposed within the F_3 families selected for higher 1000 KW under heat stress produced significant positive response in the five F_4 populations (Table 5). The % of responses ranged from 9.47 to 18.18% of populations mean with an average of 12.02%. The average stem diameter over the five populations increased from 5.31 mm for the un selected bulks to 5.96 mm in the F_4 selections denoting 12.24% increase. The realized heritability values ranged from 0.33 to 0.92 which was remarkably high.

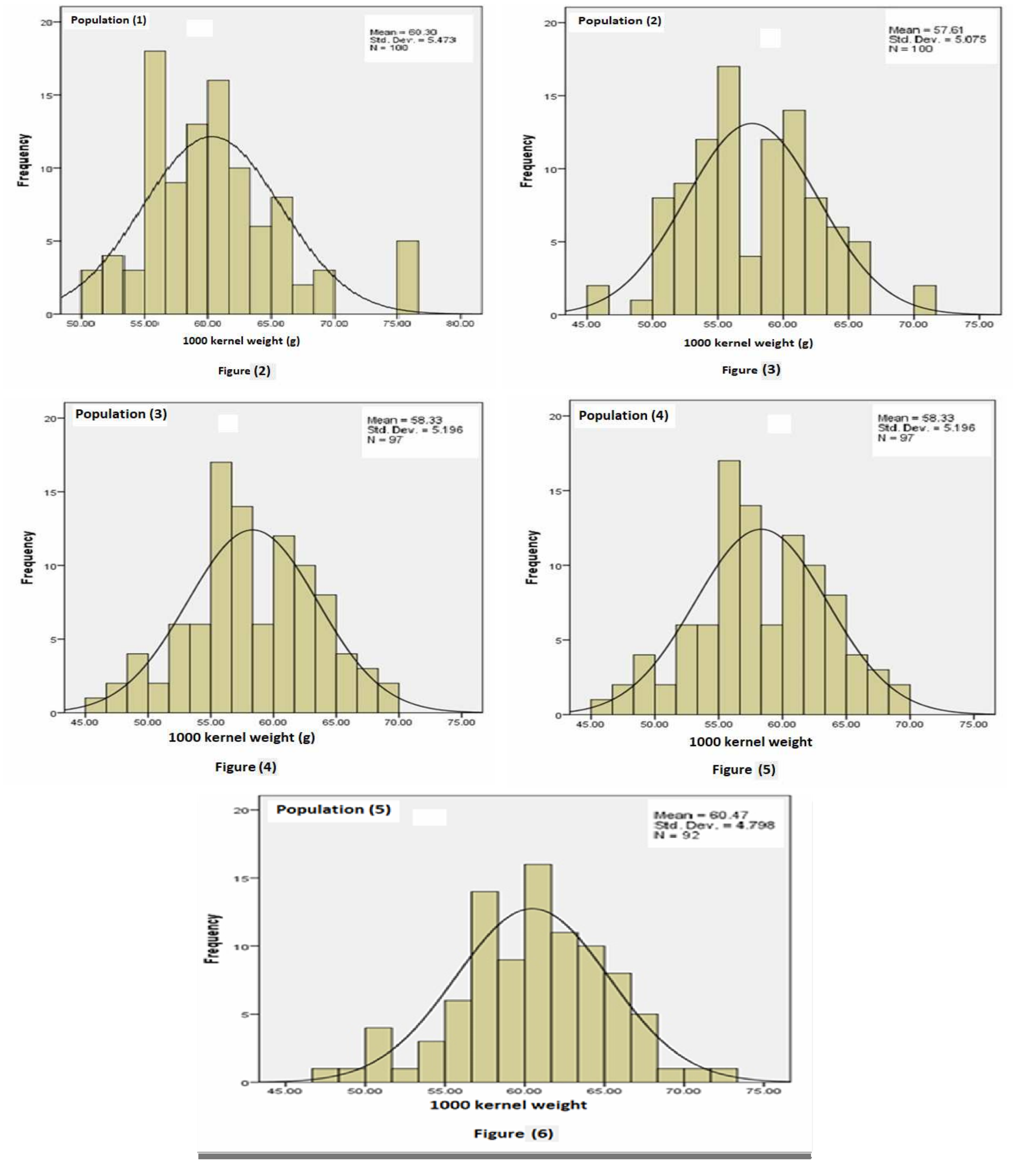
Selection for stem diameter resulted in concurrent positive response in 1000 KW in the five populations which were highly significant in four of which ranged from 11.33 to 20.41% of populations mean with an average of 16.24 % (Table 5).

Table 4. Means of stem diameter of the five F_4 populations under heat stress conditions as well as means of the selected plants for higher stem diameter and the selection differential.

Pop. No.	F_3 mean (bulk)	F_3 selected	Selection differential
1	5.70	6.89	1.19
2	5.18	6.75	1.57
3	4.95	5.97	1.02
4	5.17	5.85	0.68
5	5.66	6.37	0.71
Average	5.33	6.36	1.03

Average over the five populations, the mean 1000 KW increased from 49.33 g for the bulks to 55.99 g for the F_4 selection marking 16.01% average increase in grain filling capacity.

Correlated positive response was also obtained with selection for stem diameter in grain yield /spike which ranged from 11.41 to 24.76 % with an average of 19.5 % (Table 5). The over populations average of grain yield /spike increased due to selection for stem diameter from 4.40 g for the bulks to 6.1g for the F_4 selections marking 38.6% average increase.



Figs. 2-6. Frequency distributions of 1000 KW of the five populations under heat stress.

Table 5. Means of the bulks and F_4 selected families for stem diameter with the responses (R%) in the five populations together with the means and correlated responses (CR) for 1000 KW and grain yield /spike.

Pop. NO.	Pop. type	Stem diameter		1000 KW		Grain yield /spike	
		Mean(mm)	R%	Mean (g)	CR%	Mean (g)	(CR) %
1	Selected	6.24	9.47**	58.42	20.20 **	5.61	24.66**
	Bulk	5.70		48.60		4.50	
	h^2 realized	0.45					
2	Selected	5.70	10.03 **	56.95	11.33**	5.39	24.76**
	Bulk	5.18		51.15		4.32	
	h^2 realized	0.33					
3	Selected	5.85	18.18 **	60.53	11.62**	6.17	21.21**
	Bulk	4.95		54.23		5.09	
	h^2 realized	0.88					
4	Selected	5.80	12.18**	53.20	20.41**	6.44	11.41**
	Bulk	5.17		44.18		5.78	
	h^2 realized	0.92					
5	Selected	6.24	10.25**	53.00	17.68**	6.95	15.45**
	Bulk	5.66		45.03		6.02	
	h^2 realized	0.81					

P < 0.05 and ** P < 0.01

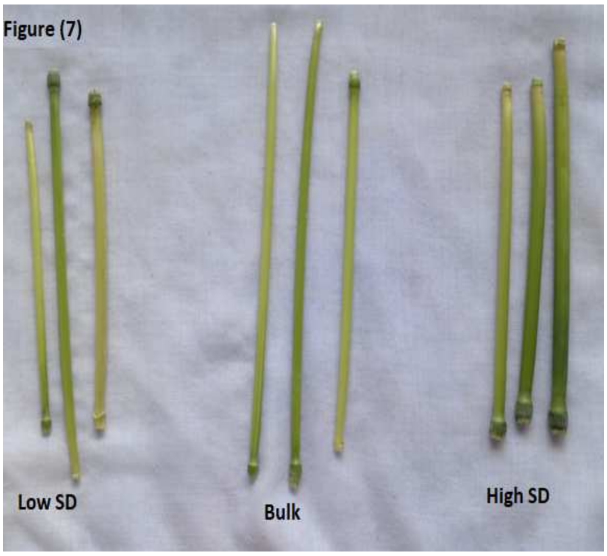


Figure 7. Photograph of the second basal internode of the bulk and F_3 selections for high and low 1000 KW under heat stress.

Discussion: -

Tolerance to heat stress in wheat has been enhanced through improving grain filling capacity by selection under high temperature either directly for kernel weight or indirectly for stem diameter. The significant response to selection for higher 1000 KW under heat stress was greater in the hot environment (averaged 6.9% of population mean) than under favorable conditions (4.9% on average). These results conform to the principle of Jinks and Connolly (1973) in that for improving performance in a specific environment, selection must be conducted in that environment. This principle was also experimentally validated by Ceccarelli *et al.* (1998) who reported that improving grain yield in barley under stress conditions was most effectively done by direct selection under stress. Apparently, selection for higher kernel weight under heat stress is a form of antagonistic selection in which selection pressure acts in the opposite direction of the environment which is expected to increase the mean performance and reduce environmental sensitivity (Falconer, 1990). Evidently, the F_3 families selected for higher 1000 KW under heat stress were more tolerant and less sensitive to high temperature since it displayed less reduction due to heat stress (averaged 5.55%) than the unselected bulks (average reduction of 7.14%).The fact that the F_3 families selected for lower 1000 KW showed greater reduction in the favorable environment (averaged 5.6 %) in than under heat stress (averaged 4.12%) validates the principles of Jinks and Connolly (1973) that synergistic selection, where selection pressure and the environment act in the same direction, reduces the mean performance and increases environmental sensitivity. The concurrent positive responses obtained in stem diameter with selection for higher 1000 KW under heat stress were also greater under high temperature (averaged 8.82%) than under favorable condition (averaged 7.15%) which lend further support to the expectations of Falconer (1990) and indicates that the two characters are closely related (Omara *et al.*, 2009 and Kassem, 2016). This was also substantiated by the fact that direct selection for stem diameter employed in the second cycle produced concurrent responses in 1000 KW which was greater (averaged 16.24%) than that produced by selecting for 1000 KW itself (averaged 8.82%). Thus, selection for 1000 KW under heat stress produced correlated responses in stem diameter and vice versa which indicates the crucial role of stem diameter in sustaining grain filling under high temperature. According to Kassem (2016), stem diameter is correlated with number of vascular bundles and consequently with the storage capacity of the stem for WSC which will be remobilized to the developing grains under heat stress. Storage capacity for stem reserves has been reported by Blum (1998) to be related to stem volume and to increase with longer stem and greater stem specific weight. In this study the long spike inbred lines used as parents of the F_2 populations were so chosen as to be of equal height (>120 cm) and hence of equal stem length in order to confine the variation in the segregating generation to that due to stem diameter. Accordingly, the concurrent positive responses obtained in 1000 KW (averaged 16.01%) as well as in grain yield/spike (averaged 19.5%) with selection for stem diameter can be attributed to the contribution of this character to the storage capacity of the stem and hence to grain filling under heat stress. Evidently, grain yield per spike under late season stress conditions was reported to be most related to stem diameter in wheat (Okoyama *et al*, 2005). The obvious conclusion of this study is that enhancing heat tolerance in wheat can be achieved by selecting for stem diameter under heat stress which is an easily measurable character in large populations with minimum effort, cost or time.

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الإستجابة للإنتخاب للقدرة على ملء الحبوب في قمح الخبز تحت الإجهاد الحراري

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تم التحسين للتحمل الحراري لقمح الخبز عبر تحسين القدرة على ملء الحبوب بواسطة دورتي انتخاب متتابعتين تم ممارستهما على خمس عشائر جيل ثاني مشتقة من تهجينات بين سلالات طويلة السنبلة متماثلة الطول تتفارق في وزن الألف حبة ، تحت الإجهاد الحراري لموعد الزراعة المتأخر عند شدة انتخاب قدرها 5% وتم قياس الإستجابة تحت البيئة المواتية وبيئة الإجهاد الحرارى. وقد أوضحت النتائج ما يلى: 1- حدوث استجابات معنوية موجبة في وزن الألف حبة بالعشائر الخمسة وكانت الإستجابة أعلى تحت بيئة الإجهاد الحرارى (6.9% من متوسط العشيرة) عنها تحت الظروف المواتية (4.9%).2- كانت عائلات الجيل الثالث المنتخبة لوزن الألف حبة الأعلى أقل حساسية للإجهاد الحرارى حيث أظهرت انخفاضا أقل (5.55%) عن العشائر غير المنتخبة (7.14% انخفاضاً) بالمقارنة بالأداء في البيئة المواتية. 3- كانت الإستجابة للإنتخاب لوزن الألف حبة المنخفض أكبر تحت البيئة المواتية (بمتوسط 5.6%) عنه تحت الإجهاد الحرارى (بمتوسط 4.12%).4- حدثت استجابات متلازمة معنوية في قطر الساق حيث كانت أكبر مع الإنتخاب لزيادة وزن الألف حبة تحت الإجهاد الحرارى (بمتوسط 8.82%) عن تحت البيئة المواتية (بمتوسط 4.12%).5- الإنتخاب الإتجاهي في الدورة الثانية لقطر الساق أنتج استجابة معنوية في العشائر الخمس بمتوسط 16.24% من متوسط العشيرة كما نتج عنه استجابة متلازمة في وزن الألف حبة بمتوسط 16.01% وفى محصول الحبوب بالسنبلة بمتوسط 19.5%.6- الإنتخاب لوزن الألف حبة أدى إلى استجابة متلازمة في قطر الساق والعكس كان صحيحا مما يعنى أن الصفتين على علاقة قوية ببعضهما. 7- كان الإنتخاب لقطر الساق أكثر كفاءة عن الإنتخاب لوزن الألف حبة في تحسين القدرة على ملء الحبوب عبر توفير قدرة تخزينية أكبر لمخزون الساق من الكربوهيدرات الذائبة التي سيتم تحريكها إلى الحبوب المتكونة تحت ظروف الإجهاد الحرارى.